

The Complexity of Finding Multiple Solutions to Betweenness and Quartet Compatibility

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Abstract

We show that two important problems that have applications in computational biology are ASP-complete, which implies that, given a solution to a problem, it is NP-complete to decide if another solution exists. We show first that a variation of BETWEENNESS, which is the underlying problem of questions related to radiation hybrid mapping, is ASP-complete. Subsequently, we use that result to show that QUARTET COMPATIBILITY, a fundamental problem in phylogenetics that asks whether a set of quartets can be represented by a parent tree, is also ASP-complete. The latter result shows that Steel’s QUARTET CHALLENGE, which asks whether a solution to QUARTET COMPATIBILITY is unique, is coNP-complete.

1 Introduction

Many biological problems focus on synthesizing data to yield new information. We focus on the complexity of two such problems. The first is motivated by radiation hybrid mapping (RH mapping) [10] which was developed to construct long range maps of mammalian chromosomes (e.g. [1, 8, 17]). Roughly, RH mapping uses x-rays to break the DNA into fragments and gives the relative order of DNA markers on the fragments [10]. The underlying computational problem is to assemble these fragments into a single strand (i.e., a “linear order”). As Chor and Sudan [7] show, the assembly of these fragments can be modeled by the well-known decision problem BETWEENNESS. Loosely speaking, this problem asks if there exists a total ordering over a set of elements that satisfies a set of constraints, each specifying one element to lie between two other elements (see Section 2 for a more detailed definition). Since this

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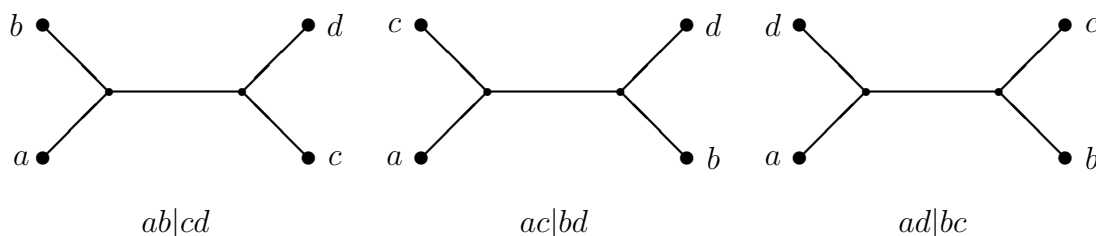
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classical problem is NP-complete [22], Chor and Sudan [7] developed a polynomial-time approximation. Their algorithm, by using a geometric approach, either returns that no betweenness ordering exists or returns such an ordering that satisfies at least one half of the given constraints. However, in the context of RH mappings, one usually knows the so-called 3' and 5' end of the DNA under consideration. Therefore, we consider a variation of BETWEENNESS—called CBETWEENNESS—whose instances do not only contain a collection of constraints, but also an explicit specification of the first and last DNA marker, and that asks whether or not there exists a total ordering whose first and last element coincide with the first and last DNA marker, respectively. In this paper, we are particularly interested in the following question related to CBETWEENNESS: given a solution to an instance of CBETWEENNESS, is there another solution? A positive answer to this question may imply that the sampling of relatively ordered DNA markers is not large enough to determine the correct ordering of the entire set of DNA markers.

Our second question focuses on finding the optimal phylogenetic tree for a set of taxa (e.g. species). Under the most popular optimization criteria (maximum parsimony and maximum likelihood), it is NP-hard to find the optimal tree [13, 24]. Despite the NP-hardness, several approaches to this problem exist, one of which finds a phylogenetic tree by splitting the problem into subproblems, solves the subproblems and then recombines the solutions to form a complete phylogenetic tree that represents all taxa under consideration [4, 6, 19]. To this end, quartets which are phylogenetic trees on 4 taxa are often used. Given 4 taxa, there are three possible ways to arrange them:



Since the number of possible topologies grows exponentially with the number of taxa, it is easier to decide the arrangement or topology of each subset of 4 taxa than the topology for a large set of taxa. This leads to the question: how hard is it to build a tree from quartets? If Q denotes the set of all quartets of a phylogenetic tree T , then T is uniquely determined by Q and can be reconstructed in polynomial time [12]. However, in most cases T is not given, and Q is often incomplete (i.e. there exists a set of 4 taxa for which no quartet is given) or elements in Q contradict each other. In such a case, it is NP-complete to decide whether there exists a phylogenetic tree on n taxa that *displays* Q [27]; that is, a phylogenetic tree that explains all the ancestral relationships given by the quartets, where n is the number of taxa over all elements in Q . Because of the NP-completeness of this latter problem—called QUARTET COMPATIBILITY—algorithmic approaches are rare. Nevertheless, several attractive graph-theoretic characterizations of the problem exist [16, 25]. While [25] approaches the problem by using a chordal-graph characterization on an underlying intersection graph, [16] establishes a so-called quartet graph and edge colorings

via this graph to decide whether or not there exists a phylogenetic tree that displays a given set of quartets. As a follow-up on this last question, Steel asks whether or not the following problem, called the **QUARTET CHALLENGE**, is NP-hard [28]: given a set Q of quartets over n taxa and a phylogenetic tree T on n taxa that displays Q , is T the unique such tree that displays Q ? Although the above-mentioned characterizations [16, 25] comprises several results on when a set of quartets is displayed by a unique phylogenetic tree, the computational complexity of the **QUARTET CHALLENGE** remains open. We note that if a set Q of quartets that does not contain any redundant information is displayed by a unique phylogenetic tree on n taxa, then the minimum size of Q is $n - 3$ [26, Corollary 6.3.10] while the current largest maximum size is $2n - 8$ [11].

To investigate the computational complexity of problems for when a solution is given and one is interested in finding another solution, Yato and Seta [30] developed the framework of **ANOTHER SOLUTION PROBLEMS (ASP)**. Briefly, if a problem is ASP-complete, then given a solution to a problem, it is NP-complete to decide if a distinct solution exists. Many canonical problems are ASP-complete, such as several variations of satisfiability, as well as games like Sudoku [30].

In this paper, we show that, given a solution to an instance of **CBETWEENNESS** or **QUARTET COMPATIBILITY**, finding a second solution is ASP-complete. To show that **CBETWEENNESS** is ASP-complete, we use a reduction from a variant of satisfiability, namely, **NOT-ALL-EQUAL-3SAT WITH CONSTANTS** (see Section 2 for a detailed definition). Using this result, we establish a second reduction that subsequently shows that **QUARTET COMPATIBILITY** is also ASP-complete. As we will soon see, the ASP-completeness of **QUARTET COMPATIBILITY** implies coNP-completeness of the **QUARTET CHALLENGE**.

We note that while this paper was in preparation, a preprint was released [18] that addresses the complexity of the **QUARTET CHALLENGE** using different techniques than employed here.

This paper is organized as follows: Section 2 details background information from complexity theory and phylogenetics. Section 3 gives the two reduction results, and Section 4 contains some concluding remarks.

2 Preliminaries

This section gives an outline of the ASP-completeness concept and formally states the decision problems that are needed for this paper. Preliminaries in the context of phylogenetics are given in the second part of this section.

2.1 Computational complexity

Notation and terminology introduced in this section follows [14] and [30], with the former being an excellent reference for general complexity results.

ASP-completeness. The notion of *ASP-completeness* was first published by Yato and Seta [30]. Their paper provides a theoretical framework to analyze the computational complexity of problems whose input contains, among others, a solution to a given problem instance, and the objective is to find a distinct solution to that instance or to return that no such solution exists. To this end, the authors use *function problems* whose answers can be more complex in contrast to decision problems that are always answered with either ‘yes’ or ‘no’. Formally, the complexity class *FNP* contains each function problem Π that satisfies the following two conditions:

- (i) There exists a polynomial p such that the size of each solution to a given instance ψ of Π is bounded by $p(\psi)$.
- (ii) Given an instance ψ of Π and a solution s , it can be decided in polynomial time if s is a solution to ψ .

Note that the complexity class *FNP* is a generalization of the class *NP* and that each function problem in *FNP* has an analogous decision problem.

Now, let Π and Π' be two function problems. We say that a polynomial-time reduction f from Π to Π' is an *ASP-reduction* if for any instance ψ of Π there is a bijection from the solutions of ψ to the solutions of $f(\psi)$, where $f(\psi)$ is an instance of Π' that has been obtained under f . Note that, while each ASP-reduction is a so-called ‘parsimonious reduction’, the converse is not necessarily true. Parsimonious reductions have been introduced in the context of enumeration problems (for details, see [23]). Furthermore, a function problem Π' is *ASP-complete* if and only if $\Pi' \in \text{FNP}$ and there is an ASP-reduction from Π to Π' for any function problem $\Pi \in \text{FNP}$.

Remark. Throughout this paper, we prove that several problems are ASP-complete. Although these problems are stated as decision problems in the remainder of this section, it should be clear from the context which associated function problems we consider. More precisely, for a decision problem Π_d , we consider the function problem Π whose instance ψ consists of the same parameters as an instance of Π_d and, additionally, of a solution to ψ , and whose question is to find a distinct solution that fulfills all conditions given in the question of Π_d . Hence, if Π is ASP-complete, then this implies that, unless $\text{P}=\text{NP}$, it is computationally hard to find a second solution to an instance of Π .

Satisfiability (SAT) problems. The satisfiability problem is a well-known problem in the study of computational complexity. In fact, it was the first problem shown to be NP-complete [14, 9]. Before we can formally state the problem, we need some definitions. Let $V = \{x_1, x_2, \dots, x_n\}$ be a set of variables. A *literal* is either a variable x_i or its negation \bar{x}_i , and a *clause* is a disjunction of literals. Now let C be a conjunction of clauses (for an example, consider the four clauses given in Figure 1). A *truth assignment* for C assigns each literal to either *true* or *false* such that, for each $i \in \{1, 2, \dots, n\}$, $x_i = \text{true}$ if and only if $\bar{x}_i = \text{false}$. We say that a literal is *satisfied* (resp. *falsified*) if its truth value is *true* (resp. *false*).

$$\begin{array}{ll}
C_1 : x_1 \vee x_2 \vee x_3 & \sigma_0 : \{x_1, x_2, x_3, x_4\} \rightarrow \text{true} \\
C_2 : x_1 \vee \bar{x}_3 \vee x_4 & \sigma_1 : \{x_1, x_2\} \rightarrow \text{true}; \sigma_1 : \{x_3, x_4\} \rightarrow \text{false} \\
C_3 : \bar{x}_1 \vee x_3 \vee \bar{x}_4 & \sigma_2 : \{x_1, x_3, x_4\} \rightarrow \text{true}; \sigma_2 : \{x_2\} \rightarrow \text{false} \\
C_4 : x_2 \vee \bar{x}_3 \vee x_4 &
\end{array}$$

Figure 1: Left: An example of 4 clauses on the variables x_1, \dots, x_4 . Right: Truth assignments to the non-negated literals. As an instance of 3SAT, there are several possible satisfying truth assignments including σ_0 , σ_1 , and σ_2 . When viewed as an instance of NAE-3SAT, σ_0 is not satisfying since it assigns all literals of the first clause C_1 to *true*, violating the ‘not all equal’ condition.

Problem: SATISFIABILITY

Instance: A set of variables V and a conjunction C of clauses over V .

Question: Does there exist a truth assignment for C such that each clause contains at least one literal assigned to *true*?

3SAT is a special case of the general SAT problem in which each clause of a given instance contains exactly three literals. Referring back to Figure 1, all three truth assignments σ_0 , σ_1 , and σ_2 satisfy the four clauses for when regarded as an instance of 3SAT. The next theorem is due to [30, Theorem 3.5].

Theorem 2.1. *3SAT is ASP-complete.*

We will next show the ASP-completeness of another version of SAT that is similar to the following decision problem.

Problem: NOT-ALL EQUAL-3SAT (NAE-3SAT)

Instance: A set of variables V and a conjunction C of 3-literal clauses over V .

Question: Is there a truth assignment such that for each clause there is a literal satisfied and a literal falsified by the assignment?

As an example, see Figure 1, and note that σ_0 does not satisfy the four clauses when regarded as an instance of NAE-3SAT. It is an immediate consequence of the definition of NAE-3SAT that, given a solution S to an instance, a second solution to this instance can be calculated in polynomial time by taking the complement of S ; that is assigning each literal to *true* (resp. *false*) if it is assigned to *false* (resp. *true*) in S (see [21]).

The next decision problem can be obtained from NAE-3SAT by allowing for instances that contain the constants T or F .

Problem: NOT-ALL EQUAL-3SAT WITH CONSTANTS (cNAE-3SAT)

Instance: A set of variables V , constants T and F , and a conjunction C of 3-literal clauses over $V \cup \{T, F\}$.

Question: Is there a truth assignment such that the constants T and F are assigned *true* and *false*, respectively, and for each clause, there is a literal or constant satisfied and a literal or constant falsified by the assignment?

In the case of cNAE-3SAT, we cannot always obtain a second solution from a first one by taking its complement. For instance, if an instance of cNAE-3SAT contains the clause $a_k \vee b_k \vee T$, then the assignment $a_k = b_k = \text{false}$ is valid, while the complementary assignment $a_k = b_k = \text{true}$ is not. In fact, we next show that cNAE-3SAT is ASP-complete.

Theorem 2.2. *cNAE-3SAT is ASP-complete.*

Proof. Regarding cNAE-3SAT as a function problem (see the remark earlier in this section), it is easily seen that deciding if a truth assignment to an instance of cNAE-3SAT satisfies this instance takes polynomial time. Hence, cNAE-3SAT is in FNP. Now, let ψ be an instance of the APS-complete problem 3SAT over the variables $V = \{x_1, \dots, x_n\}$. To show that cNAE-3SAT is ASP-complete we reduce ψ to an instance ψ' of cNAE-3SAT over an expanded set of variables $V' = V \cup \{x_{n+1}, \dots, x_{n+m}\}$, where m is the number of clauses in ψ . Let x_{n+k} be a new variable chosen for the clause $(a_k \vee b_k \vee c_k)$ of ψ . We obtain ψ' from ψ by replacing each clause $(a_k \vee b_k \vee c_k)$ with the following 4 clauses:

$$(a_k \vee b_k \vee x_{n+k}) \wedge (\bar{x}_{n+k} \vee c_k \vee F) \wedge (a_k \vee x_{n+k} \vee T) \wedge (b_k \vee x_{n+k} \vee T).$$

Clearly, this reduction can be done in polynomial time. The size of ψ' is polynomial in the size of ψ , and a straightforward check shows that ψ is satisfiable if and only if ψ' is satisfiable. Furthermore, for each clause, x_{n+k} is uniquely determined by the truth values of a_k and b_k , since the reduction makes \bar{x}_{n+k} equivalent to $a_k \vee b_k$. Hence, each truth assignment that satisfies ψ can be mapped to a unique valid truth assignment of ψ' . Consequently, the converse; i.e. each truth assignment of ψ' is mapped to a unique truth assignment of ψ , also holds. It now follows that the described reduction from 3SAT to cNAE-3SAT is an ASP-reduction, thereby completing the proof of this theorem. \square

The BETWEENNESS problem. The decision problem BETWEENNESS, that we introduce next, asks whether or not a given finite set can be totally ordered such that a collection of constraints which are given in form of triples is satisfied.

Problem: BETWEENNESS

Instance: A finite set A and a collection C of ordered triples (a, b, c) of distinct elements from A such that each element of A occurs in at least one triple from C .

Question: Does there exist a *betweenness ordering* f of A for C ; that is a one-to-one function $f : A \rightarrow \{1, 2, \dots, |A|\}$ such that for each triple (a, b, c) in C either $f(a) < f(b) < f(c)$ or $f(c) < f(b) < f(a)$?

Loosely speaking, for each triple (a, b, c) , the element b lies between a and c in a betweenness ordering of A for C . BETWEENNESS has been shown to be NP-complete [22]. Similar to NAE-3SAT, notice that if there is a solutions, say $a_1 < a_2 < \dots < a_s$, to an instance of BETWEENNESS, then there is always a second solution $a_s < \dots < a_2 < a_1$ to that instance that can clearly be calculated in polynomial time. Therefore, BETWEENNESS is not ASP-complete.

We next introduce a natural variant of BETWEENNESS—called CBETWEENNESS—that is ASP-complete (see Section 3.1). An instance of CBETWEENNESS differs from an instance of BETWEENNESS in a way that the former contains two constants, say m and M , and each betweenness ordering has m as its first and M as its last element. We say that m is the *minimum* and M the *maximum* of each betweenness ordering.

Problem: CBETWEENNESS

Instance: A finite set A and a collection C of ordered triples (a, b, c) of distinct elements from $A \cup \{M, m\}$ with $m, M \notin A$ such that each element of $A \cup \{M, m\}$ occurs in at least one triple from C .

Question: Does there exist a *betweenness ordering* f of $A \cup \{M, m\}$ for C such that f is a one-to-one function $f : A \cup \{m, M\} \rightarrow \{0, 1, 2, \dots, |A| + 1\}$ such that for each triple (a, b, c) in C either $f(a) < f(b) < f(c)$ or $f(c) < f(b) < f(a)$, and $f(m) = 0$ and $f(M) = |A| + 1$?

Although an instance ψ of CBETWEENNESS can have several betweenness orderings, note that if $a_0 < a_1 < a_2 < \dots < a_{|A|+1}$ is a betweenness ordering for ψ with $a_0 = m$ and $a_{|A|+1} = M$, then $a_{|A|+1} < \dots < a_2 < a_1 < a_0$ is not such an ordering. This is because m must be the minimal element, and M the maximal.

2.2 Phylogenetics

This section provides preliminaries in the context of phylogenetics. For a more thorough overview, we refer the interested reader to Semple and Steel [26].

Phylogenetic trees and subtrees. An *unrooted phylogenetic X -tree* T is a connected acyclic graph whose leaves are bijectively labeled with elements of X and have degree 1. Furthermore, T is *binary* if each non-leaf vertex has degree 3. The set X is the *label set* of T and denoted by $L(T)$.

Now let T be an unrooted phylogenetic X -tree, and let X' be a subset of X . The *minimal subtree* of T that connects all elements in X' is denoted by $T(X')$. Furthermore, the *restriction* of T to X' , denoted by $T|X'$, is the phylogenetic tree obtained from $T(X')$ by contracting degree-2 vertices.

Throughout this paper, we will use the terms ‘unrooted phylogenetic tree’ and ‘phylogenetic tree’ interchangeably.

Quartets. A *quartet* is an unrooted binary phylogenetic tree with exactly four leaves. For example, let q be a quartet whose label set is $\{a, b, c, d\}$. We write $ab|cd$ (or equivalently, $cd|ab$) if the path from a to b does not intersect the path from c to d . Similarly to the label set of a phylogenetic tree, $L(q)$ denotes the label set of q , which is $\{a, b, c, d\}$. Now, let $Q = \{q_1, q_2, \dots, q_n\}$ be a set of quartets. We write $L(Q)$ to denote the union $L(q_1) \cup L(q_2) \cup \dots \cup L(q_n)$.

Compatibility. Let T be a phylogenetic tree whose leaf set is a superset of $L(q)$. Then T displays q if q is isomorphic to $T|L(q)$. Furthermore, T displays a set Q of quartets if T displays each element of Q , in which case Q is said to be *compatible*. Lastly, $\langle Q \rangle$ denotes the set of all unrooted binary phylogenetic trees that display Q and whose label set is precisely $L(Q)$.

The concept of compatibility leads to the following decision problem, which has been shown to be NP-complete [27].

Problem: QUARTET COMPATIBILITY

Instance: A set Q of quartets.

Question: Is Q compatible?

The next problem has originally been posed by Steel [28] and is a natural extension of QUARTET COMPATIBILITY.

Problem: QUARTET CHALLENGE

Instance: A binary phylogenetic X -tree T and a set Q of quartets on X such that T displays Q .

Question: Is T the unique phylogenetic X -tree that displays Q ?

Remark. Given a binary phylogenetic X -tree T and a set Q of quartets on X such that T displays Q , deciding whether another solution exists is the complement question of the QUARTET CHALLENGE. That is, a *no* answer to an instance of the first question translates to a *yes* answer to the same instance of the QUARTET CHALLENGE and vice versa.

We end this section by highlighting the relationship between the two problems QUARTET CHALLENGE and QUARTET COMPATIBILITY. Let Q be an instance of QUARTET COMPATIBILITY. If Q is compatible, then there exists an unrooted phylogenetic tree T with label set $L(Q)$ that displays Q . This naturally leads to the question whether T is the unique such tree on $L(Q)$, which is exactly the question of the QUARTET CHALLENGE. To make progress towards resolving the complexity of this challenge, we will first show that QUARTET COMPATIBILITY is ASP-complete. Thus, by [30, Theorem 3.4], the decision problem that corresponds to QUARTET COMPATIBILITY, i.e. asking whether another solution exists, is NP-complete. Now, recalling the last remark, this in turn implies that the QUARTET CHALLENGE is coNP-complete. Lastly, note that if T is the unique tree with label set $L(Q)$ that displays Q , then T is binary.

3 ASP-Completeness Results

3.1 ASP-Reduction for cBETWEENNESS

In this section, we focus on establishing an ASP-reduction from cNAE-3SAT to cBETWEENNESS. This reduction gives that cBETWEENNESS is ASP-complete (see Theorem 3.1). We note that, by a similar argument, we can also reduce NAE-3SAT to BETWEENNESS.

Let ψ be an instance of cNAE-3SAT consisting of a conjunction of 3-literal clauses $\{a_k \vee b_k \vee c_k : 1 \leq k \leq l\}$, on the set of variables $\{x_1, \dots, x_n\}$ and a subset of the constants $\{T, F\}$. Let $\{-x_1, -x_2, \dots, -x_n, x_1, x_2, \dots, x_n\}$ be the set of corresponding literals of ψ , where $-x_i$ (instead of \bar{x}_i) denotes the negation of x_i . We next build an instance ψ' of cBETWEENNESS.

In the following, we think of an ordering as setting symbols on a line segment where the symbol X is the center; i.e. X represents ‘0’. Furthermore, we refer to the region left of X as the *negative side* and to the region right of X as the *positive side* of the line segment. For every variable x_i with $i \in \{1, 2, \dots, n\}$, we preserve the two symbols x_i and $-x_i$ and introduce two new symbols M_i and $-M_i$ which are auxiliary symbols that mark the midpoints between the x_i and $-x_i$ symbols (see Figure 2). Moreover, if T or F is contained in any clause of ψ , then we also introduce the symbol M and m , respectively, such that M represents the largest and m the smallest value on the line segment (for details, see below). Intuitively, if the literal x_i is assigned to *true*, then the symbol x_i is assigned to the positive side and the symbol $-x_i$ to the negative side. Otherwise, if the literal x_i is assigned to *false*, then the symbol x_i is assigned to the negative side and the symbol $-x_i$ to the positive side.

The following triples fix X as ‘0’. For every $i \leq n$, they put x_i and $-x_i$ on either side of X . They also put M_i and $-M_i$ on either side of X .

$$\begin{aligned} (-x_i, X, x_i) & \quad \text{for all } i \text{ such that } 1 \leq i \leq n \\ (-M_i, X, M_i) & \quad \text{for all } i \text{ such that } 1 \leq i \leq n \end{aligned} \tag{1}$$

The next set of triples put an order between the x_i and M_i symbols. They establish that $|x_i| < |x_{i+1}|$ for every $i, 1 \leq i < n$, where we interpret $|\cdot|$ to be the distance to X (i.e. ‘0’) under the induced ordering. Also, they fix M_i and $-M_i$ as middle points between x_i (or $-x_i$), and x_{i-1} (or $-x_{i-1}$) (see Figure 2).

$$\begin{aligned} (-M_i, x_{i-1}, M_i) & \quad (-M_i, -x_{i-1}, M_i) & \text{for all } i \text{ such that } 2 \leq i \leq n \\ (-x_i, M_i, x_i) & \quad (-x_i, -M_i, x_i) & \text{for all } i \text{ such that } 1 \leq i \leq n \end{aligned} \tag{2}$$

We will require that either both x_i and M_i are on the positive side, or on the negative side.

$$(x_i, X, -M_i) \quad (-x_i, X, M_i) \quad \text{for all } i \text{ such that } 1 \leq i \leq n \tag{3}$$

Original Encoding: Given a clause $(a_k \vee b_k \vee c_k)$ of ψ , we assume for the remainder of Section 3.1 that $a_k \in \{-x_i, x_i\}$, $b_k \in \{-x_{i'}, x_{i'}\}$, and $c_k \in \{-x_{i''}, x_{i''}\}$ such that $i < i' < i''$. Since there are at most two constants per clause, we also assume that a_k is never a constant and that, if b_k is a constant, then c_k is a constant. Lastly, we assume that the whole set of clauses of ψ is ordered lexicographically.

To guarantee the ‘not-all-equal’ condition, we use the original encoding of Opatrny [22]. For each clause $a_k \vee b_k \vee c_k$ with $k \in \{1, 2, \dots, l\}$, we add a new symbol, Z_k , where l is the number of clauses in ψ . We add the following triples that correspond to the original encoding of Opatrny [22]:

$$(a_k, Z_k, b_k) \quad (c_k, X, Z_k) \quad \text{for all } k \text{ such that } 1 \leq k \leq l. \tag{4}$$

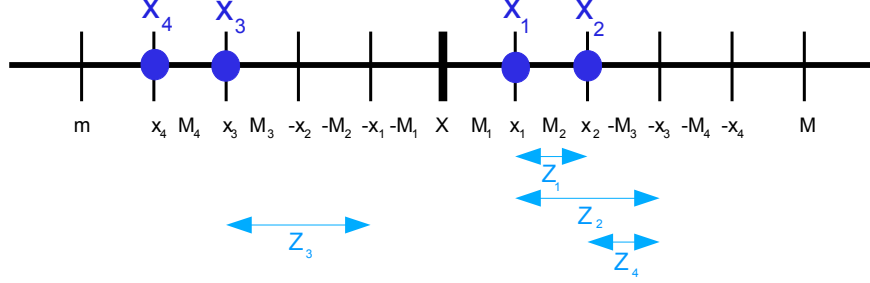


Figure 2: A mapping of the first set of clauses under the truth assignment σ_1 from Figure 1. The top blue variables are the initial variables from the instance of cNAE-3SAT. For a given truth assignment, the ordering of the x_i and M_i symbols is fixed by the triples in Equation 1-4. However, without additional triples (and auxiliary symbols), the Z_i symbols have overlapping ranges (as indicated by the lines with arrows) and, as such, several possible orderings for a single truth assignment.

If a clause contains a constant F or T , it gets substituted by m or M , respectively, in the triple. For instance, a clause $a_k \vee b_k \vee T$ generates the two triples (a_k, Z_k, b_k) , (T, X, Z_k) . These triples force Z_k to be on the negative side.

The triples of Equation 4 say that at least one of the literals of the k^{th} clause is assigned to *true* and one to *false* (see Figure 2). When viewed in terms of the possible truth assignment to the variables in the original clause, the truth assignment $a_k = b_k = c_k = \text{true}$ is eliminated since for all three initial literals to be assigned *true*, both c_k and Z_k would be assigned to the positive side of X violating the second triple of Equation 4. By a similar argument, the truth assignment $a_k = b_k = c_k = \text{false}$ is eliminated. This leaves six other possible satisfying truth assignments.

The triples of Equation 1-4 are not sufficient to prove ASP-completeness of cBETWEENNESS since different orderings of cBETWEENNESS can be reduced to the same satisfying truth assignment of the cNAE-3SAT instance (see Figure 2). This happens since the symbols in $\{Z_1, Z_2, \dots, Z_l\}$ are not fixed with respect to the x_i and $-x_i$ symbols or to one another. In what follows, we will show how to fix the ordering of these symbols.

Fixing Auxiliary Symbols in the Ordering of the Initial Symbols: We next introduce new symbols $-Z_1, \dots, -Z_l$, where l is the number of clauses in ψ . From now on, we will establish a set of triples for every clause. We assume that the triples up to the $(k-1)^{th}$ clause have been defined, and now we will give the set of triples of the k^{th} clause. The intuition is that we want $-Z_k$ to be opposite to Z_k with respect to X . We add:

$$(-a_k, -Z_k, -b_k) \quad (-c_k, X, -Z_k) \quad (5)$$

To fix the position of Z_k and $-Z_k$ for every $1 \leq k \leq l$ relative to the x_i and M_i symbols, we need more triples. Recall that $a_k \in \{-x_i, x_i\}$. We add the following triples saying that

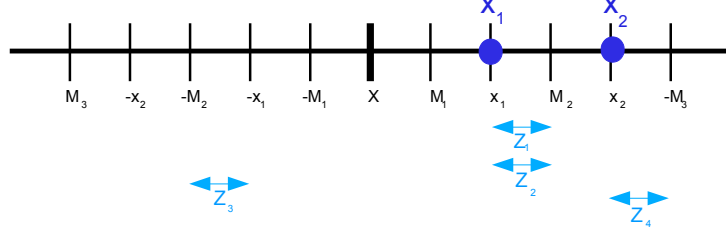


Figure 3: Equations 6-7 limit the ranges of the Z_k symbols but do not completely fix the ordering. Continuing the example from Figure 1, we show the possible ordering for the σ_1 truth assignment. Note that the order of Z_1 and Z_2 is not fixed and additional triples (and variables) are needed.

$$|Z_k| < |M_{i+1}|. \quad (-M_{i+1}, Z_k, M_{i+1}) \quad (-M_{i+1}, -Z_k, M_{i+1}) \quad (6)$$

The following triples say that $|M_i| < |Z_k|$.

$$(-Z_k, M_i, Z_k) \quad (-Z_k, -M_i, Z_k) \quad (7)$$

These triples eliminate the interval $[-M_i, M_i]$ for the positions of Z_k and $-Z_k$, respectively. Since the M_i symbols occur as midpoints between the x_i symbols, we have restricted each Z_k to be ‘near’ a_k or $-a_k$; i.e. Z_k is ‘near’ $-x_i$ or x_i on the line segment. As a consequence of Equations 6, we have $|M_i| < |Z_k| < |x_i|$ or $|x_i| < |Z_k| < |M_{i+1}|$. At this point, we have the symbols Z_k and $-Z_k$ in a tight interval between consecutive positions, except for the truth assignments $a_k = c_k = \text{false}$ and $b_k = \text{true}$, and $a_k = c_k = \text{true}$ and $b_k = \text{false}$. In these cases, both $|M_i| < |Z_k| < |x_i|$ and $|x_i| < |Z_k| < |M_{i+1}|$, are still possible. See Figure 3 for an example. We therefore add:

$$(Z_k, -a_k, c_k) \quad (-Z_k, a_k, -c_k) \quad (8)$$

which fixes the Z_k such that $|x_i| < |Z_k| < |M_{i+1}|$.

Fixing the Order of Auxiliary Symbols Among Themselves: With the Z_k and $-Z_k$ being fixed around x_i and $-x_i$, respectively, and recalling that $a_i \in \{-x_i, x_i\}$, we need to address the case where the first literal of several clauses is either x_i or $-x_i$. Note that these corresponds to consecutive clauses of ψ since ψ is ordered lexicographically. In this case, we will use extra auxiliary symbols to nest the Z_k symbols around x_i and $-x_i$. The intuition for these clauses is to partition the consecutive intervals into distinct regions for the different Z_k and $-Z_k$ symbols (see Figure 4).

Let the k^{th} clause be $a_k \vee b_k \vee c_k$ and assume that it is not the only clause starting by x_i or $-x_i$. We will add the symbols $L_k, -L_k, U_k, -U_k$ to create 4 new subintervals (two around x_i and two around $-x_i$) where we will fix Z_k and $-Z_k$. Also, we will add the new symbols Y_k to be the mirror image of Z_k with respect to x_i (or $-x_i$), and $-Y_k$ to be the mirror image of $-Z_k$ with respect to x_i (or $-x_i$).

The following triples express that the symbols Z_k , Y_k , L_k and U_k are all placed on the positive side, or in the negative side, and similarly for the negated symbols $-Z_k$, $-Y_k$, $-L_k$ and $-U_k$.

$$\begin{array}{ll} (Z_k, X, -Y_k) & (-Z_k, X, Y_k) \\ (Z_k, X, -L_k) & (-Z_k, X, L_k) \\ (Z_k, X, -U_k) & (-Z_k, X, U_k) \end{array} \quad (9)$$

First, if the k^{th} clause is the first clause in the ordering that starts by x_i or $-x_i$, we need the following triples saying that $|x_i| < |U_k|$ and $|L_k| < |x_i|$.

$$\begin{array}{ll} (-U_k, x_i, U_k) & (-U_k, -x_i, U_k) \\ (-x_i, L_k, x_i) & (-x_i, -L_k, x_i) \end{array} \quad (10)$$

Second, if the k^{th} clause is not the first one in the ordering that has x_i or $-x_i$ as its first literal (i.e. $a_{k-1}, a_k \in \{-x_i, x_i\}$), we proceed by introducing the following triples. By induction, we assume that for the previous $(k-1)^{st}$ clause, the subintervals were created using L_{k-1} and U_{k-1} with the corresponding Z_{k-1} and Y_{k-1} in them. In this case, we need the triples saying that $|Z_{k-1}| < |U_k|$ and $|Y_{k-1}| < |U_k|$ (instead of the first two triples of Equation 10):

$$\begin{array}{ll} (-U_k, Z_{k-1}, U_k) & (-U_k, -Z_{k-1}, U_k) \\ (-U_k, Y_{k-1}, U_k) & (-U_k, -Y_{k-1}, U_k) \end{array} \quad (11)$$

and the triples saying that $|L_k| < |Z_{k-1}|$ and $|L_k| < |Y_{k-1}|$ (instead of the last two triples of Equation 10).

$$\begin{array}{ll} (-Z_{k-1}, L_k, Z_{k-1}) & (-Z_{k-1}, -L_k, Z_{k-1}) \\ (-Y_{k-1}, L_k, Y_{k-1}) & (-Y_{k-1}, -L_k, Y_{k-1}) \end{array} \quad (12)$$

At this point, we have Z_{k-1} either between two consecutive L symbols, or between two consecutive U symbols. The same is true for $-Z_{k-1}$, Y_{k-1} and $-Y_{k-1}$.

Now, we need triples to locate Z_k , $-Z_k$, Y_k and $-Y_k$ in the newly created intervals. We add triples saying that L_k and U_k are between Y_k and Z_k , and similarly for the negated symbols.

$$\begin{array}{ll} (Z_k, U_k, Y_k) & (Z_k, L_k, Y_k) \\ (-Z_k, -U_k, -Y_k) & (-Z_k, -L_k, -Y_k) \end{array} \quad (13)$$

Since the L and U symbols are nested around x_i and $-x_i$, this puts the Y_k and Z_k symbols in their corresponding region around x_i and $-x_i$.

Finally, we need to keep the Z_k , $-Z_k$, Y_k , and $-Y_k$ from being too far from x_i or $-x_i$ and intruding in the region of x_{i+1} , $-x_{i+1}$, x_{i-1} , or $-x_{i-1}$. This was done already for the Z_k and $-Z_k$ symbols in Equations 6 and 7, and now we will do it for the Y_k and $-Y_k$ symbols. This is important in the case that the k^{th} clause is the last one containing x_i or $-x_i$ as its first literal. To do this, we need additional clauses saying that $|M_i| < |Y_k|$ and $|Y_k| < |M_{i+1}|$.

$$\begin{array}{ll} (Y_k, M_i, -Y_k) & (Y_k, -M_i, -Y_k) \\ (M_{i+1}, Y_k, -M_{i+1}) & (M_{i+1}, -Y_k, -M_{i+1}) \end{array} \quad (14)$$

Theorem 3.1. *CBETWEENNESS is ASP-complete.*

Proof. Given a 3CNF instance of cNAE-3SAT $\{a_k \vee b_k \vee c_k : 1 \leq k \leq l\}$, on the set of variables $\{x_1, \dots, x_n\}$ and a subset of the constants $\{T, F\}$, we can create an instance of cBETWEENNESS by using Equations 1-14. We show how to build a bijection between satisfying truth assignments for the formula instance and betweenness orderings that are solution to the cBETWEENNESS instance.

To define the total betweenness orderings, we consider the line segment $[-n-1, n+1]$ and define a mapping ϕ_σ for every truth assignment σ of the variables x_1, \dots, x_n . While the domain of σ is $\{x_1, \dots, x_n\}$, the domain of ϕ_σ , $S = \text{dom}(\phi_\sigma)$, is contained in

$$\{x_1, \dots, x_n, -x_1, \dots, -x_n, m, M, X, M_1, \dots, M_n, -M_1, \dots, -M_n, \\ Z_1, \dots, Z_l, -Z_1, \dots, -Z_l, Y_1, \dots, Y_l, -Y_1, \dots, -Y_l, \\ L_1, \dots, L_l, -L_1, \dots, -L_l, U_1, \dots, U_l, -U_1, \dots, -U_l\}.$$

The mapping ϕ_σ of truth assignments to orderings can now be defined the following way. First as a general property of ϕ_σ , let us say that $\phi_\sigma(-x) = -\phi_\sigma(x)$, for every symbol x of the instance. If $\sigma(x_i) = T$, then $\phi_\sigma(x_i) = i$ (and $\phi_\sigma(-x_i) = -i$), and otherwise $\phi_\sigma(x_i) = -i$ (and $\phi_\sigma(-x_i) = i$). At this point the symbols, x_i and $-x_i$ get fixed in the interval $[-n, n]$ on opposite sides of 0. Note that the symbol X represents 0 in the ordering, that is, $\phi_\sigma(X) = 0$. This part of the definition of ϕ_σ fulfills Equation 1. Next, we put m below $-n$, and M above n (i.e. $\phi_\sigma(m) = -n-1$ and $\phi_\sigma(M) = n+1$), as is required for the definition of a betweenness ordering for cBETWEENNESS.

Next, we define the ordering function for the M_i symbols. If $\phi_\sigma(x_i) > 0$, then $\phi_\sigma(M_i) = \phi_\sigma(x_i) - 1/2$ and $\phi_\sigma(-M_i) = \phi_\sigma(-x_i) + 1/2$. If $\phi_\sigma(x_i) < 0$, then $\phi_\sigma(M_i) = \phi_\sigma(x_i) + 1/2$ and $\phi_\sigma(-M_i) = \phi_\sigma(-x_i) - 1/2$. This definition fulfills Equations 2 and 3.

Now, for every $k, 1 \leq k \leq l$, we have to fix the position of every Z_k under the mapping ϕ_σ . Recall that each clause $a_k \vee b_k \vee c_k$ is ordered from smaller to larger index. We begin with the case where only this clause begins with the variable represented by a_k . Then, no additional auxiliary variables (i.e. Y_k , L_k , and U_k) were introduced, and only Z_k has to be placed in the order. There are six cases based on possible truth values assigned to a_k , b_k , and c_k (as noted above, $a_k = b_k = c_k = \text{false}$ and $a_k = b_k = c_k = \text{true}$ are no satisfying truth assignments for an instance of cNAE-3SAT. If $\sigma(a_k) = \sigma(c_k)$ and $\sigma(b_k)$ has the opposite value (i.e. the cases of $a_k = c_k = \text{false}$ and $b_k = \text{true}$, and $a_k = c_k = \text{true}$ and $b_k = \text{false}$), then Z_k will be set around $-\phi_\sigma(a_k)$, since the Equations 5 and 6, the fact that the index of b_k is bigger than that of a_k , and the fact that we have the triple (Z_k, X, c_k) of Equation 3. Note that the triples in Equation 7 fix the positions of $\phi_\sigma(Z_k)$ to one side of $-\phi_\sigma(a_k)$. For the remaining cases where $\sigma(a_k) \neq \sigma(c_k)$ we define ϕ_σ to place Z_k near $\phi_\sigma(a_k)$, again by Equations 3, 5, and 6. The general definition is as follows:

$$\phi_\sigma(Z_k) = \begin{cases} \phi_\sigma(a_k) + \frac{1}{4} & \text{if } \sigma(a_k) \neq \sigma(c_k) \text{ and } \sigma(b_k) = \text{true} \\ \phi_\sigma(a_k) - \frac{1}{4} & \text{if } \sigma(a_k) \neq \sigma(c_k) \text{ and } \sigma(b_k) = \text{false} \\ \phi_\sigma(-a_k) + \frac{1}{4} & \text{if } \sigma(a_k) = \sigma(c_k) \text{ and } \sigma(b_k) = \text{true} \\ \phi_\sigma(-a_k) - \frac{1}{4} & \text{if } \sigma(a_k) = \sigma(c_k) \text{ and } \sigma(b_k) = \text{false} \end{cases}$$

If there is only one clause beginning with a given literal or its negation, then by the triples in Equations 1 to 9, all the symbols (as well as their negations) are fixed.

There might be a number of clauses with the same variable in the first position of the disjunction. The positions of these respective Z_k 's have to be fixed, as well as the auxiliary variables, L_k , U_k and Y_k 's. By the triples in Equations 12, 13 and 14 the auxiliary variables L_k and U_k (and the negative ones) are nested around $\phi_\sigma(a_k)$ and $\phi_\sigma(-a_k)$ forming intervals, and Z_k and Y_k are set inside intervals of consecutive L_k 's or consecutive U_k 's (see Figure 4). We assume that this is the p^{th} clause that begins with the same variable. Then, as above, the exact placement of these variables depends on σ . Define ϕ_σ as follows:

- Case 1: $\sigma(a_k) = false$, $\sigma(b_k) = false$, $\sigma(c_k) = true$:

$$\begin{aligned}\phi_\sigma(L_k) &= \phi_\sigma(a_k) + \frac{p}{2l} & \phi_\sigma(U_k) &= \phi_\sigma(a_k) - \frac{p}{2l} \\ \phi_\sigma(Z_k) &= \phi_\sigma(a_k) - \frac{2p+1}{4l} & \phi_\sigma(Y_k) &= \phi_\sigma(a_k) + \frac{2p+1}{4l}\end{aligned}$$

- Case 2: $\sigma(a_k) = false$, $\sigma(b_k) = true$, $\sigma(c_k) = false$:

$$\begin{aligned}\phi_\sigma(L_k) &= -\phi_\sigma(a_k) - \frac{p}{2l} & \phi_\sigma(U_k) &= -\phi_\sigma(a_k) + \frac{p}{2l} \\ \phi_\sigma(Z_k) &= -\phi_\sigma(a_k) + \frac{2p+1}{4l} & \phi_\sigma(Y_k) &= -\phi_\sigma(a_k) - \frac{2p+1}{4l}\end{aligned}$$

- Case 3: $\sigma(a_k) = false$, $\sigma(b_k) = true$, $\sigma(c_k) = true$:

$$\begin{aligned}\phi_\sigma(L_k) &= \phi_\sigma(a_k) + \frac{p}{2l} & \phi_\sigma(U_k) &= \phi_\sigma(a_k) - \frac{p}{2l} \\ \phi_\sigma(Z_k) &= \phi_\sigma(a_k) + \frac{2p+1}{4l} & \phi_\sigma(Y_k) &= \phi_\sigma(a_k) - \frac{2p+1}{4l}\end{aligned}$$

- Case 4: $\sigma(a_k) = true$, $\sigma(b_k) = false$, $\sigma(c_k) = false$:

$$\begin{aligned}\phi_\sigma(L_k) &= \phi_\sigma(a_k) - \frac{p}{2l} & \phi_\sigma(U_k) &= \phi_\sigma(a_k) + \frac{p}{2l} \\ \phi_\sigma(Z_k) &= \phi_\sigma(a_k) - \frac{2p+1}{4l} & \phi_\sigma(Y_k) &= \phi_\sigma(a_k) + \frac{2p+1}{4l}\end{aligned}$$

- Case 5: $\sigma(a_k) = true$, $\sigma(b_k) = false$, $\sigma(c_k) = true$:

$$\begin{aligned}\phi_\sigma(L_k) &= -\phi_\sigma(a_k) + \frac{p}{2l} & \phi_\sigma(U_k) &= -\phi_\sigma(a_k) - \frac{p}{2l} \\ \phi_\sigma(Z_k) &= -\phi_\sigma(a_k) - \frac{2p+1}{4l} & \phi_\sigma(Y_k) &= -\phi_\sigma(a_k) + \frac{2p+1}{4l}\end{aligned}$$

- Case 6: $\sigma(a_k) = true$, $\sigma(b_k) = true$, $\sigma(c_k) = false$:

$$\begin{aligned}\phi_\sigma(L_k) &= \phi_\sigma(a_k) - \frac{p}{2l} & \phi_\sigma(U_k) &= \phi_\sigma(a_k) + \frac{p}{2l} \\ \phi_\sigma(Z_k) &= \phi_\sigma(a_k) + \frac{2p+1}{4l} & \phi_\sigma(Y_k) &= \phi_\sigma(a_k) - \frac{2p+1}{4l}\end{aligned}$$

For each of these cases, it can be easily checked that the auxiliary variables satisfy Equations 9-14.

We have shown that given a satisfying truth assignment σ , there exists a mapping, $\phi_\sigma : S \rightarrow [-n-1, n+1]$. This mapping induces a natural ordering on S that we will call $f_\sigma : S \rightarrow [0, |S|+1]$. For $s_1, s_2 \in S$,

$$f_\sigma(s_1) < f_\sigma(s_2) \iff \phi_\sigma(s_1) < \phi_\sigma(s_2).$$

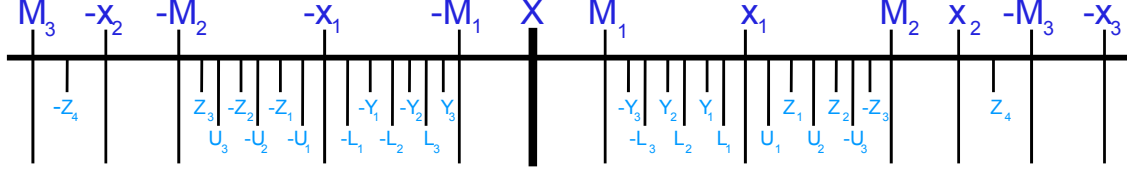


Figure 4: Equations 9-14 fix the locations of the Z symbols, as well as the auxiliary variables uniquely in the order. Above illustrates the location of these auxiliary symbols for the σ_1 truth assignment from Figure 1.

Note that this fixes the minimal and maximal elements, m and M so that $f_\sigma(m) = 0$ and $f_\sigma(M) = |S| + 1$. Further, we note that f_σ satisfies Equations 1-14, since ϕ_σ satisfied them and has the same ordering. We note that, by construction, each satisfying truth assignment, σ , uniquely defines f_σ . This construction can be done in quadratic time in $|S|$. Since the number of auxiliary variables in S is bounded polynomially in n , we have a polynomial time reduction from cNAE-3SAT to cBETWEENNESS.

Now we need to show the converse. Given a betweenness ordering on S that satisfies all the triples obtained from an instance, we need to define an assignment that for every clause, there is one literal satisfied and one literal falsified. We define the assignment as follows. For all symbols x_i (resp. $-x_i$) such that $f(x_i) > f(X)$ (resp. $f(-x_i) > f(X)$), we assign x_i (resp. $-x_i$) to *true*. Similarly, for all symbols x_i (resp. $-x_i$) such that $f(x_i) < f(X)$ (resp. $f(-x_i) < f(X)$), we assign x_i (resp. $-x_i$) to *false*. Furthermore, let m be the constant F , and let M be the constant T . Now, we have to see that the assignment obtained satisfies at least one literal, and falsifies at least one literal of every clause. Equation 5 ensures that for a given clause $a_k \vee b_k \vee c_k$, not all three literals can be to the right of X or to the left of X . Therefore, the assignment created from the ordering will set at least one literal to *true* and at least one literal to *false*. Lastly, we note that if two betweenness orderings on S , f_1 and f_2 , yield identical truth assignments on $\{x_1, \dots, x_n\}$, then, by Equations 1-4, f_1 and f_2 agree on the ordering of $\{x_1, \dots, x_n, -x_1, \dots, -x_n, m, M, X\}$. Further, Equations 5-14 fix the remainder auxiliary variables, and as such, we must have $f_1 = f_2$. \square

3.2 The Quartet Challenge is coNP-complete

In this section, we show that the QUARTET CHALLENGE is coNP-complete. To this end, we extend the original argument of Steel [27, Theorem 1] that showed that the related question, QUARTET COMPATIBILITY, is NP-complete. He reduced BETWEENNESS to QUARTET COMPATIBILITY by mapping a betweenness ordering to a caterpillar tree (for a definition, see below). Under that reduction, multiple solutions to an instance ψ of the QUARTET COMPATIBILITY problem could correspond to a single solution of the BETWEENNESS instance that is obtained by transforming ψ . To prove that the QUARTET CHALLENGE is coNP-complete, we extend Steel's polynomial-time reduction from BETWEENNESS to an ASP-reduction from

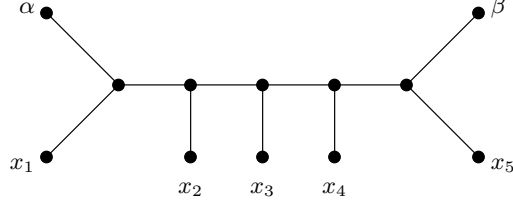


Figure 5: The caterpillar $\alpha x_1 | x_2 x_3 x_4 | x_5 \beta$.

C BETWEENNESS to QUARTET COMPATIBILITY.

We first give some additional definitions. Let A be a finite set, and let C be a set of ordered triples of elements from A . Let (x, y) be a pair of elements of A such that no triple of C contains x and y . We say that (x, y) is a *lost pair* with regards to A and C .

Let T be an unrooted phylogenetic tree. A pair of leaves (a, b) of T is called a *cherry* (or *sibling pair*) if a and b are leaves that are adjacent to a common vertex of T . Furthermore, T is a *caterpillar* if T is binary and has exactly two cherries. Following [27], we say that T is an $\alpha\beta$ -caterpillar, if α and β are leaves of distinct cherries of T . We write $\alpha x_1 | x_2 x_3 \dots x_{n-1} | x_n \beta$ to denote the caterpillar whose two cherries are (α, x_1) and (x_n, β) , and, for each $i \in \{1, 2, \dots, n\}$, the path from α to x_i consists of $i + 1$ edges. Now, let $\alpha x_1 | x_2 x_3 \dots x_{n-1} | x_n \beta$ be an $\alpha\beta$ -caterpillar. For each $i, j \in \{1, 2, \dots, n\}$ with $i \neq j$, we say that the path from x_i to x_j *crosses* x_k if and only if $i < k < j$ or $j < k < i$. For example, Figure 5 shows an $\alpha x_1 | x_2 x_3 x_4 | x_5 \beta$ -caterpillar whose path from x_1 to x_4 crosses x_2 and x_3 .

Before we prove the main result of this section (Theorem 3.3), we need a lemma.

Lemma 3.2. *Let T be a phylogenetic tree, and let $ab|cd$ be a quartet that is displayed by T . Then no element of $\{(a, c), (a, d), (b, c), (b, d)\}$ is a cherry of T .*

Proof. By the definition of a quartet, the path from a to b in T does not intersect the path from c to d in T . Thus, no element of $\{(a, c), (a, d), (b, c), (b, d)\}$ is a cherry of T . \square

Theorem 3.3. QUARTET COMPATIBILITY is ASP-complete.

Proof. We start by noting that it clearly takes polynomial time to decide whether or not a phylogenetic tree T displays a given set Q of quartets since it is sufficient to check if $T|L(q) \cong q$ for each quartet q in Q . Hence, QUARTET COMPATIBILITY is in FNP.

To show that QUARTET COMPATIBILITY is ASP-complete, we next describe an ASP-reduction from C BETWEENNESS to QUARTET COMPATIBILITY. Let ψ be an instance of C BETWEENNESS over a finite set $A = \{a_1, a_2, \dots, a_s\} \cup \{m, M\}$. Let $C = \{\pi_1, \pi_2, \dots, \pi_n\}$ be the set of triples of ψ , with $\pi_i = (b_i, c_i, d_i)$ for each $i \in \{1, 2, \dots, n\}$, such that each element of $A \cup \{m, M\}$ is contained in at least one triple. Recall that m is the first and M the last element of each betweenness ordering f of $A \cup \{m, M\}$ for C ; that is $f(m) = 0$ and $f(M) = |A| + 1$. For simplicity throughout this proof, let $A' = A \cup \{m, M\}$. Furthermore, let $L = \{\tau_{n+1}, \tau_{n+2}, \dots, \tau_{n'}\}$ precisely be the set of all lost pairs with regards to A' and C , where $\tau_i = (x_i, y_i)$ for each $i \in \{n + 1, n + 2, \dots, n'\}$.

We next describe six sets of quartets:

1. Each triple $\pi_i = (b_i, c_i, d_i)$ in C is represented by 6 quartets in

$$Q_1 = \bigcup_{i=1}^n Q_{\pi_i} = \bigcup_{i=1}^n \{p_i p'_i | b_i c_i, p_i b_i | c_i d_i, p_i c_i | d_i q_i, p_i d_i | q_i q'_i, \alpha p_i | p'_i \beta, \alpha q_i | q'_i \beta\}.$$

2. Each lost pair $\tau_i = (x_i, y_i)$ in L is represented by 5 quartets in

$$Q_2 = \bigcup_{i=n+1}^{n'} Q_{\tau_i} = \bigcup_{i=n+1}^{n'} \{p_i p'_i | x_i y_i, p_i x_i | y_i q_i, p_i y_i | q_i q'_i, \alpha p_i | p'_i \beta, \alpha q_i | q'_i \beta\}.$$

3. Let $a_j, a_k \in A'$, and let a be any fixed element of A . Set Q_3 , Q_4 , and Q_5 to be the following:

$$Q_3 = \bigcup_{i=2}^{n'} \bigcup_{j=1}^{i-1} \{p_i p'_i | p_j a, p_i p'_i | p'_j a, q_i q'_i | q_j a, q_i q'_i | q'_j a\},$$

$$Q_4 = \bigcup_{i=1}^{n'} \bigcup_{j=1}^{n'} \{p_i p'_i | q_j q'_j, p_i p'_i | q_j a, p_i p'_i | q'_j a\}, \text{ and}$$

$$Q_5 = \bigcup_{i=1}^{n'} \bigcup_{j=2}^{s+2} \bigcup_{k=1}^{j-1} \{p_i p'_i | a_j a_k, q_i q'_i | a_j a_k\}.$$

4. Let $a_i, a_j \in A$, and set Q_6 to be the following:

$$Q_6 = \bigcup_{i=2}^s \bigcup_{j=1}^{i-1} \{\alpha m | a_i a_j, a_i a_j | M \beta\}.$$

Noting that n' is in the order of $O(|A|^3)$, the quartet set

$$Q = \bigcup_{i=1}^6 Q_i$$

can be constructed in polynomial time.

We note that for Steel's original proof [27, Theorem 1], in which he describes a polynomial-time reduction from BETWEENNESS to QUARTET COMPATIBILITY in order to show that the latter decision problem is NP-complete, the construction of Q_1 is sufficient.

A straightforward analysis of the quartets in Q_{π_i} and Q_{τ_i} , respectively, shows that $\langle Q_{\pi_i} \rangle$ and $\langle Q_{\tau_i} \rangle$ contain the following phylogenetic trees which are all $\alpha\beta$ -caterpillars:

$$\langle Q_{\pi_i} \rangle = \{\alpha p_i | p'_i b_i c_i d_i q_i | q'_i \beta, \alpha q_i | q'_i d_i c_i b_i p_i | p'_i \beta\}$$

for each $i \in \{1, 2, \dots, n\}$ and

$$\langle Q_{\tau_i} \rangle = \{\alpha p_i | p'_i x_i y_i q_i | q'_i \beta, \alpha q_i | q'_i y_i x_i p_i | p'_i \beta\}$$

for each $i \in \{n+1, n+2, \dots, n'\}$.

Let T be a phylogenetic tree of $\langle Q \rangle$. By Q_1 and Q_2 , it is easily checked that either, if p_i and p'_i are both crossed by the path from α to b_i (resp. x_i) in T , then q_i and q'_i are both crossed by the path from β to b_i (resp. x_i) in T , or if q_i and q'_i are both crossed by the path from α to b_i (resp. x_i) in T , then p_i and p'_i are both crossed by the path from β to b_i (resp. x_i) in T for when $i \in \{1, 2, \dots, n\}$ (resp. $i \in \{n+1, n+2, \dots, n'\}$). We refer to this property of T as the *desired pq-property for i* .

Let V be the set $\{p_1, \dots, p_{n'}, p'_1, \dots, p'_{n'}, q_1, \dots, q_{n'}, q'_1, \dots, q'_{n'}\}$, and let T be a phylogenetic tree in $\langle Q \rangle$. We continue with making several observations that will be important in what follows:

1. The second and third quartet in Q_1 , the second quartet in Q_2 , and Lemma 3.2 imply that T does not have a cherry (a, b) with $a, b \in A'$.
2. The quartets in Q_5 and Lemma 3.2 imply that T does not have a cherry (a, b) with $a \in A'$ and $b \in V$.
3. The last two quartets in Q_1 and Q_2 , the quartets in Q_3 , the first quartet in Q_4 , and Lemma 3.2 imply that T does not have a cherry (a, b) with $a, b \in V$.

In conclusion, T is an $\alpha\beta$ -caterpillar. This observation leads to a number of additional properties that are satisfied by T :

- (i) By Q_5 and the desired *pq-property* for each $i \in \{1, 2, \dots, n'\}$, the subtree $T(A')$ can be obtained from T by deleting exactly two of its edges.
- (ii) Let $i \in \{1, 2, \dots, n'\}$. Let P contain each element of $(\{p_1, p_2, \dots, p_{n'}, p'_1, p'_2, \dots, p'_{n'}\} - \{p_i, p'_i\})$ that is crossed by the path from p_i (and p'_i) to a in T for any $a \in A'$. Then, by Q_3 , each element in P has an index that is smaller than i . Analogously, let P' contain each element of $(\{q_1, q_2, \dots, q_{n'}, q'_1, q'_2, \dots, q'_{n'}\} - \{q_i, q'_i\})$ that is crossed by the path from q_i (and q'_i) to a in T for any $a \in A'$. Then, again by Q_3 , each element in P' has an index that is smaller than i .
- (iii) Let $a \in A'$. By the second and third quartet of Q_4 the path from q_i (and q'_i) to a does not cross an element of $\{p_1, p_2, \dots, p_{n'}, p'_1, p'_2, \dots, p'_{n'}\}$ in T for each $i \in \{1, 2, \dots, n'\}$.
- (iv) By (i)-(iii), the path from p_i (resp. q_i) to p'_i (resp. q'_i) in T consists of 3 edges for each $i \in \{1, 2, \dots, n'\}$. In particular, by the last two quartets of Q_1 and Q_2 , respectively, the path from α to p'_i (resp. q'_i) crosses p_i (resp. q_i) and the path from β to p_i (resp. q_i) crosses p'_i (resp. q'_i) in T .

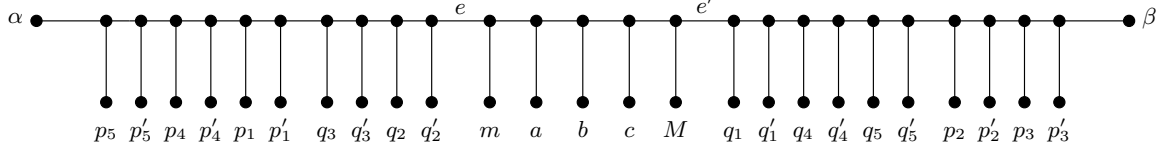


Figure 6: An $\alpha\beta$ -caterpillar in $\langle Q \rangle$ that satisfies properties (i)-(v) for an instance of CBETWEENNESS that consists of the four triples $\pi_1 = (m, a, b)$, $\pi_2 = (M, c, b)$, $\pi_3 = (c, a, m)$, and $\pi_4 = (m, b, M)$. Note that the associated set of lost pairs only contains $\tau_5 = (a, M)$. Details on how to construct Q are given in the proof of Theorem 3.3.

- (v) By Q_6 , the path from m to M crosses each element in A . Furthermore, neither the path from α to m nor the path from β to M crosses an element of A .

To illustrate, Figure 6 shows an $\alpha\beta$ -caterpillar T of $\langle Q \rangle$ and, consequently, satisfies properties (i)-(v) for an instance of CBETWEENNESS that contains the four triples $\pi_1 = (m, a, b)$, $\pi_2 = (M, c, b)$, $\pi_3 = (c, a, m)$, and $\pi_4 = (m, b, M)$. Note that $T(A')$ can be obtained from T by deleting the two edges e and e' .

Now, let T be a phylogenetic tree in $\langle Q \rangle$. Let T' be the phylogenetic tree obtained from T by interchanging α and β , and for each $i \in \{1, 2, \dots, n'\}$, interchanging p_i and p'_i , and q_i and q'_i . Noting that T' does display $Q \setminus Q_6$ but does not display Q since property (v) is not satisfied, the rest of this proof essentially consists of two claims.

Claim 1. Let T and T' be two elements of $\langle Q \rangle$. Then $T \cong T'$ if and only if $T|(A' \cup \{\alpha, \beta\}) \cong T'|(A' \cup \{\alpha, \beta\})$.

Trivially, if $T \cong T'$, then in particular $T|(A' \cup \{\alpha, \beta\}) \cong T'|(A' \cup \{\alpha, \beta\})$. To prove the claim it is therefore sufficient to show that, if $T \not\cong T'$, then $T|(A' \cup \{\alpha, \beta\}) \not\cong T'|(A' \cup \{\alpha, \beta\})$. Assume the contrary. Then there exist two distinct elements T and T' in $\langle Q \rangle$ such that $T|(A' \cup \{\alpha, \beta\}) \cong T'|(A' \cup \{\alpha, \beta\})$. Let a be an element of A' . Since both of T and T' are $\alpha\beta$ -caterpillars that satisfy properties (i)-(v), there exists an $i \in \{1, 2, \dots, n'\}$ such that the path from α to a crosses p_i and p'_i in one of T and T' , say T , while the path from α to a crosses q_i and q'_i in T' . By the desired pq -property for each i and property (i), note that the path from β to a crosses q_i and q'_i in T , and the path from β to a crosses p_i and p'_i in T' . If $i \in \{1, 2, \dots, n\}$, let $S = \{\alpha, \beta, p_i, p'_i, q_i, q'_i, b_i, c_i, d_i\}$, and if $i \in \{n+1, n+2, \dots, n'\}$, let $S = \{\alpha, \beta, p_i, p'_i, q_i, q'_i, x_i, y_i\}$. Since $T|(S - \{p_i, p'_i, q_i, q'_i\}) \cong T'|(S - \{p_i, p'_i, q_i, q'_i\})$, it now follows that either $T|S$ or $T'|S$ is not an element of $\langle Q_{\pi_i} \rangle$ (if $i \in \{1, 2, \dots, n\}$) or $\langle Q_{\tau_i} \rangle$ (if $i \in \{n+1, n+2, \dots, n'\}$); thereby contradicting that T and T' are both in $\langle Q \rangle$. This completes the proof of Claim 1.

Claim 2. Q is compatible if and only if A' has a betweenness ordering f for C with $f(m) = 0$ and $f(M) = |A| + 1$. In particular, there is a bijection from the solutions of ψ to the elements in $\langle Q \rangle$.

First, suppose that Q is compatible. Again, let T be an unrooted binary phylogenetic tree in $\langle Q \rangle$. Recall that the sets $\langle Q_{\pi_i} \rangle$ and $\langle Q_{\tau_i} \rangle$ both contain two $\alpha\beta$ -caterpillars. Thus

$$T|_{\{p_i, p'_i, q_i, q'_i, \alpha, \beta, b_i, c_i, d_i\}}$$

is isomorphic to one phylogenetic tree of $\langle Q_{\pi_i} \rangle$ for each $i \in \{1, 2, \dots, n\}$, and

$$T|_{\{p_i, p'_i, q_i, q'_i, \alpha, \beta, x_i, y_i\}}$$

is isomorphic to one phylogenetic tree of $\langle Q_{\tau_i} \rangle$ for each $i \in \{n+1, n+2, \dots, n'\}$. Noting that T is an $\alpha\beta$ -caterpillar, we next define a betweenness ordering of A' for C . Let T^* be $T|_{\{A' \cup \{\alpha, \beta\}\}}$, and define $f : A' \rightarrow \{1, 2, \dots, |A'|\}$ such that $2 + f(a_j)$ denotes the number of edges on the path from α to a_j in T^* for each $a_j \in A'$. Since T displays Q_{π_i} for each $i \in \{1, 2, \dots, n\}$ and the path from b_i to d_i crosses c_i in both phylogenetic trees of $\langle Q_{\pi_i} \rangle$, it follows that $f(b_i) < f(c_i) < f(d_i)$ or $f(d_i) < f(c_i) < f(b_i)$. Since this holds for each $\pi_i \in C$, it follows that f is a betweenness ordering of A' for C . In particular, by property (v), we have $f(m) = 0$ and $f(M) = |A| + 1$. Furthermore, by Claim 1 and the paragraph prior to Claim 1, each element of $\langle Q \rangle$ is mapped to a distinct betweenness ordering of A' for C with $f(m) = 0$ and $f(M) = |A| + 1$.

Second, suppose that A' has a betweenness ordering for C , and let f be one such ordering with $f(m) = 0$ and $f(M) = |A| + 1$. Note that f imposes an ordering on each lost pair (x_i, y_i) such that either $f(x_i) < f(y_i)$ or $f(y_i) < f(x_i)$. Furthermore, recall that $n' = |C| + |L|$ and $|A'| = s + 2$. Let T_0 be the unique $\alpha\beta$ -caterpillar, whose label set is $A' \cup \{\alpha, \beta\}$, such that the path from α to a_j in T_0 contains $2 + f(a_j)$ edges for each $a_j \in A'$. Let a be any element of A . Next, we describe the algorithm BUILD TREE that iteratively construct a series $T_1, T_2, \dots, T_{n'}$ of $\alpha\beta$ -caterpillars. Set i to be 1. To obtain T_i from T_{i-1} , proceed in the following way:

Let $P = \{p_1, p_2, \dots, p_{i-1}, p'_1, p'_2, \dots, p'_{i-1}\}$. We first define two edges e_i and e'_i in T_{i-1} . If the path from α to a in T_{i-1} crosses an element of P , let $e_i = \{u, v\}$ be the first edge on this path such that u is adjacent to a leaf labeled with an element of P and v is adjacent to a leaf labeled with an element that is not contained in P . Otherwise, choose e_i to be the edge that is incident with α . Similarly, if the path from β to a in T_{i-1} crosses an element of P , let $e'_i = \{u', v'\}$ be the first edge on this path such that u' is adjacent to a leaf labeled with an element of P and v' is adjacent to a leaf labeled with an element that is not contained in P . Otherwise, choose e'_i to be the edge that is incident with β . Note that e_i and e'_i are uniquely defined.

To obtain T_i from T_{i-1} , we consider two cases. First, if $i \in \{1, 2, \dots, n\}$ and $f(b_i) < f(c_i) < f(d_i)$, or if $i \in \{n+1, n+2, \dots, n'\}$ and $f(x_i) < f(y_i)$, subdivide the edge incident with α twice and join each of the two newly created vertices with a new leaf labeled p_i and p'_i , respectively, by introducing two new edges such that the path from α to p'_i crosses p_i . Furthermore, subdivide e'_i twice and join each of the two newly created vertices with a new leaf labeled q'_i and q_i , respectively, by introducing two new edges such that the path

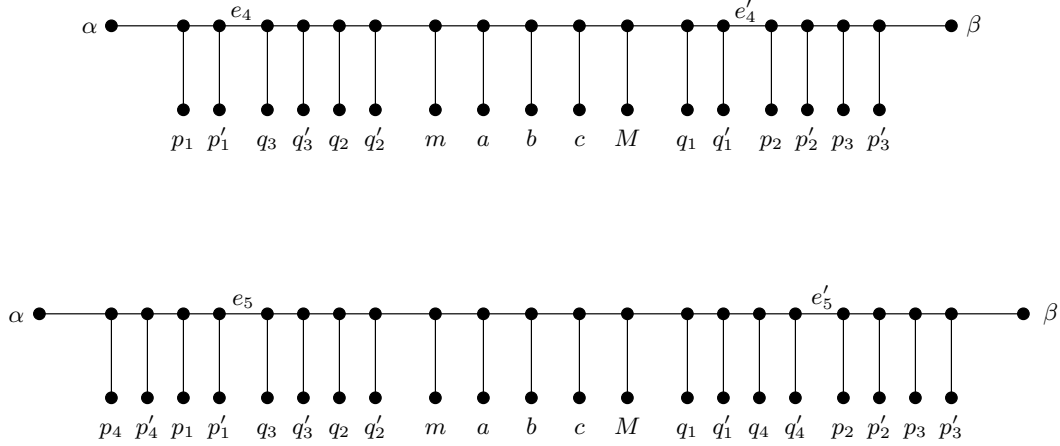


Figure 7: The intermediate trees T_3 (top) and T_4 (bottom) that are obtained from applying the algorithm BUILDTREE to the BETWEENNESS instance that is described in the caption of Figure 6 for when $m < a < b < c < M$ is the given betweenness ordering. Note that T_4 is obtained from T_3 by subdividing twice the edge that is incident with α and e'_4 , respectively. Furthermore, the tree depicted in Figure 6 is obtained from T_4 by applying one more iteration of BUILDTREE.

from β to q_i crosses q'_i . Second, if $i \in \{1, 2, \dots, n\}$ and $f(d_i) < f(c_i) < f(b_i)$, or if $i \in \{n+1, n+2, \dots, n'\}$ and $f(y_i) < f(x_i)$, subdivide e_i twice and join each of the two newly created vertices with a new leaf labeled q_i and q'_i , respectively, by introducing two new edges such that the path from α to q'_i crosses q_i . Furthermore, subdivide the edge incident with β twice and join each of the two newly created vertices with a new leaf labeled p'_i and p_i , respectively, by introducing two new edges such that the path from β to p_i crosses p'_i . A specific example of the definition of e_i and e'_i , respectively, and on how to obtain T_i from T_{i-1} is shown in Figure 7.

If $i < n'$, increment i by 1 and repeat; otherwise stop. In this way, we obtain a tree $T_{n'}$ that displays Q and, hence Q is compatible. In particular, $T_{n'}$ is an element of $\langle Q \rangle$. Furthermore, again by Claim 1 and the paragraph prior to Claim 1, $T_{n'}$ is the unique tree of $\langle Q \rangle$ that has the property that $T_{n'}|_{(A' \cup \{\alpha, \beta\})} \cong T_0$. Thus, each betweenness ordering f of A' for C with $f(m) = 0$ and $f(M) = |A| + 1$ is mapped to a distinct element of $\langle Q \rangle$. This completes the proof of Claim 2.

It now follows that the presented transformation from an instance of CBETWEENNESS to an instance of QUARTET COMPATIBILITY is an ASP-reduction that can be carried out in polynomial time. Hence, QUARTET COMPATIBILITY is ASP-complete. This establishes the proof of this theorem. \square

Now recall that ASP-completeness implies NP-completeness of the corresponding decision problem, say Π_d [30, Theorem 3.4]. Since Π_d is exactly the complementary question of the QUARTET CHALLENGE (see last paragraph of Section 2), the next corollary immediately follows.

Corollary 3.4. *The QUARTET CHALLENGE is coNP-complete.*

4 Conclusion

In this paper, we have shown that the two problems CBETWEENNESS and QUARTET COMPATIBILITY that have applications in computational biology are ASP-complete. Thus, given a betweenness ordering or a phylogenetic tree that displays a set of quartets, it is computationally hard to decide if another solution exists to a problem instance of CBETWEENNESS and QUARTET COMPATIBILITY, respectively. If there is another solution, then this may imply that a data set that underlies an analysis does not contain enough information to obtain an unambiguous result. Furthermore, by Corollary 3.4, the ASP-completeness of QUARTET COMPATIBILITY implies that the QUARTET CHALLENGE, which is one of Mike Steel’s \$100 challenges [28], is coNP-complete. Lastly, due to [30, Theorem 3.4], regardless of how many solutions to an instance of CBETWEENNESS or QUARTET COMPATIBILITY are known, it is always NP-complete to decide whether an additional solution exists.

Unless $P=NP$, the existence of efficient algorithms to exactly solve the above-mentioned two problems is unlikely. Nevertheless, there is a need to develop exact algorithms that solve small to medium sized problem instances and, most importantly, return all solutions. For example, it might be possible to start filling this gap by using fixed-parameter algorithms that have recently proven to be particularly useful to approach many questions in computational biology [15]. Alternatively, heuristics and polynomial-time approximation algorithms often provide a valuable tool to efficiently approach problem instances of larger size. While Chor and Sudan [7] established a geometric approach to approximate a betweenness ordering that satisfies at least one half of a given set of constraints, the statement of QUARTET COMPATIBILITY does not directly allow for an approximation algorithm since it is a recognition-type problem. Nevertheless, since compatible quartet sets are rare, the goal of a related problem is, given a set of quartets, to reconstruct a phylogenetic tree that displays as many quartets as possible. This problem is known as the MAXIMUM QUARTET CONSISTENCY problem. Despite its NP-hardness [3, 27], several exact algorithms (e.g. see [2, 29] and references therein) as well as a polynomial-time approximation [20] exist. It would therefore be interesting to investigate if these algorithms can be extended in a way such that they return all solutions in order to analyze whether a unique phylogenetic tree displays a given set of compatible quartets.

We end this paper by noting that the computational complexity of the QUARTET CHALLENGE changes greatly if all elements in a set of quartets over n taxa have a common taxa, say x . By rooting each quartet at x , i.e. deleting the vertex labeled x and its incident edge and regarding the resulting degree-2 vertex as the root, we obtain a set S of rooted triples (rooted phylogenetic trees on three taxa). By applying the BUILD algorithm it can now be checked in polynomial time if S is compatible [26, Proposition 6.4.4]. Furthermore, there is a unique rooted phylogenetic tree on n taxa that displays S if and only if BUILD returns a rooted binary phylogenetic tree [5, Proposition 2]. If BUILD returns a rooted phylogenetic tree that is not binary, then every refinement of this tree also displays S .

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